

FILTER-FEEDING PATTERN AND LOCAL DISTRIBUTION OF THE BRACHIOPOD, *DISCINISCA STRIGATA*

ROBERT T. PAINE

Department of Zoology, University of Washington, Seattle 5, Washington

The recent surge of interest in the functional morphology of living brachiopods has been led mainly by paleontologists, motivated by an intent to increase the reliability of their interpretations of fossil structures. Research has been focused on the mechanics of feeding, since the morphology of the filtering organ, the lophophore, and, where present, its supports, is basic to understanding the phylum's systematics. Orton (1914) contributed the first paper in this series and has been followed by Richards (1952), Atkins (1956-1961; see Rudwick, 1962, for complete citations), Chuang (1956), Williams (1956, 1960), Rudwick (1960a, 1960b, 1962), Rowell (1961), and Williams and Wright (1961). These works suggest that, with the possible exception of *Discinisca* (Rowell, 1961), all Recent brachiopods show a fair degree of convergence in the characteristics of their feeding and the fleshy portions of their lophophores. On the other hand, the functioning of "fossil" feeding mechanisms has not been agreed upon. This paper describes the filtering mechanism of the inarticulate brachiopod, *Discinisca strigata* Broderip, which, because of its uniqueness, will permit some features common to all known brachiopod filtering mechanisms to be evaluated.

MATERIAL

Large numbers of *D. strigata* were discovered living in the tidal zone near Puertecitos, Baja California, Mexico (approximately 30° 17' N.; 114° 40' W.). Field observations were made from 29 March to 1 April, 1962, principally at a station 2-3 km. north of Puertecitos, and were facilitated by an estimated 20-foot tidal range. Living specimens were successfully transported back to the Scripps Institution of Oceanography where details of the feeding process were worked out.

ECOLOGICAL OBSERVATIONS

At the principal station an extensive sand beach is interrupted at regular intervals by patches of cobbles and small boulders extending down to the low-water mark. *D. strigata* lives under the flatter of these rocks, conspicuously associated with the sponge, *Hymeniacidon adrcissiformis* Dickinson, the gastropods, *Acanthina angelica* Oldroyd, *Nerita funiculata* Menke, and *Morula ferruginosa* Reeve, and the bivalves, *Barbatia reeveana* (Orbigny) and *Isognomon chemnitzianus* (Orbigny). Whether suitable habitats in other areas can be recognized by the presence of these species is not yet known. The brachiopods often had settled in small crevices in the rocks, and occurred in microenvironments probably characterized by reduced current scour. The size distribution of the

Puertecitos population (Fig. 1), based on measurements of all specimens obtained from a large (200×50 yards) area of the cobble patch, shows no multimodality indicative of either two or more breedings or a number of year classes. The position of the normally shaped curve suggests a single prolonged spawning sometime prior to the date of collection, and that the animals may be annuals.

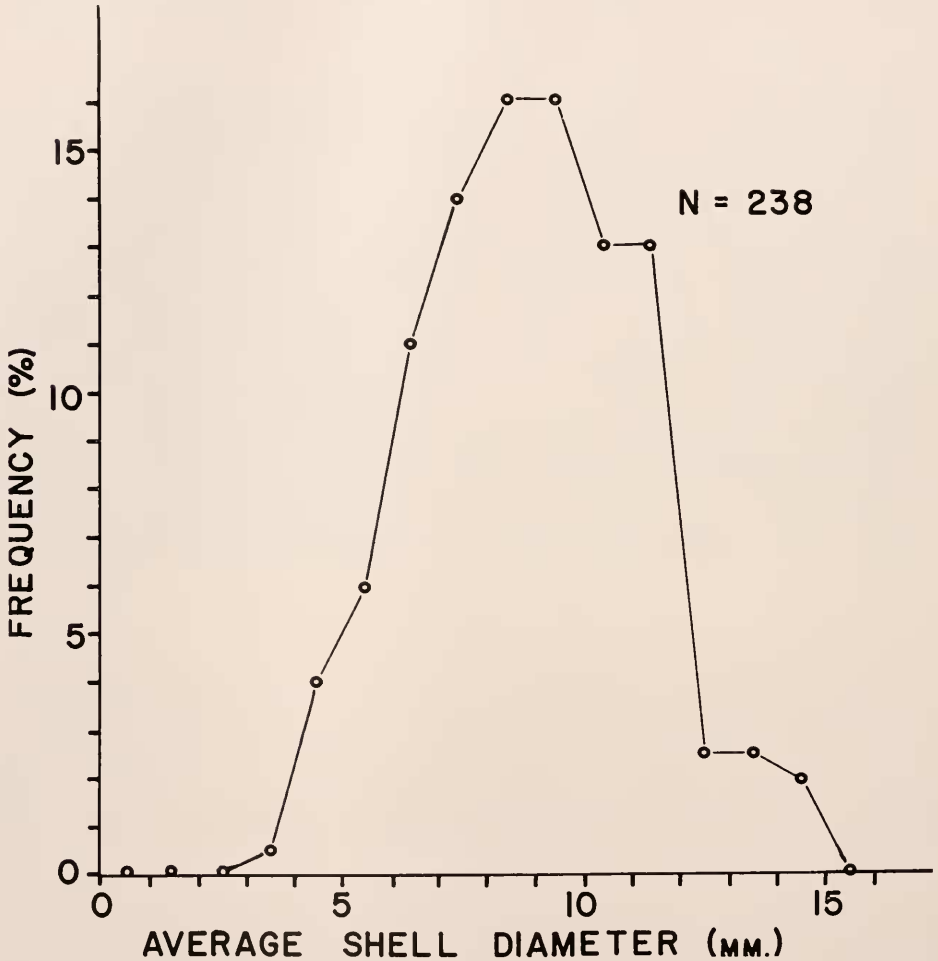


FIGURE 1. Diameter-frequency distribution of *D. strigata*. The diameter of each specimen is composed of an average of its length and width; the use of this measure is necessitated by the extremely variable individual shape.

Like many marine species, *D. strigata* shows signs of zonation. One cobble patch was completely exposed on an extreme low tide, permitting a transect to be made (Table I). Six flattish rocks, each about a foot square on their lower surface, were overturned at 10-foot intervals from the beginning of the cobble patch to the high-water mark, and the number of brachiopods seen recorded for

each interval. Brachiopod distribution was curtailed at both seaward and landward extremes, although seemingly acceptable rocks existed throughout the body of the reef. The position of this upper limit was further substantiated by two less complete transects. The lower limit cannot be explained at present, but desiccation appears to influence the upper extension. When adjacent flat rocks, high in the intertidal, were chosen such that one was slightly more elevated than the other, *D. strigata* was always under the wetter of the two rocks. Although G. A. Cooper (in Cloud, 1948) has also taken this species in intertidal water, the type was dredged from 18 fathoms (Broderip, 1833). Zonation at Puertecitos may thus be a local phenomenon, or possibly the type was collected at an atypical depth.

The evidence is substantial that this species, unlike other discinids, never forms clusters of many individuals. From collections at three Baja California locations, San Felipe, Puertecitos, and Bahia de Los Angeles (Courtesy of B. N. Kobayashi) 11, 238, and 2 specimens, respectively, were scanned with a microscope. Although

TABLE I

Zonation of D. strigata based on a transect. Numbers indicate the quantity of brachiopods observed under 6 flat rocks in each 10-foot interval. Distances are given in feet from the high-water mark. The vertical excursion is approximately 20 feet.

Distance	0-160		170	180	190	200	210	220	
Numbers	0	1	0	5	20	25	12	6	
Distance	230	240	250	260	270	280	290	300	
Numbers	5	7	11	17	0	3	3	2	
Distance	310	320	330	340	350-500				
Numbers	2	1	1	1	0				

all degrees of incrustation existed, no small brachiopods were observed. In addition, by inference the type specimens from Guatemala were collected singly (Broderip, 1833) as were those obtained by G. A. Cooper (personal communication) near Matzatlan, Mexico. On the other hand, clusters of *D. lamellosa* and *D. laevis* are well-documented (Davidson, 1888), implying the existence of distinctive differences in larval settling behavior within the genus. Blochmann (1908) has suggested that discinid clustering was associated with poor dispersal powers. It seems as probable, however, in light of an increased knowledge of the role of site selection exercised by certain larvae (Wilson, 1958), that the intrageneric variation stems from differences in settling behavior.

FILTER-FEEDING MECHANISM

Hyman (1959) has cited the extensive and varied elaboration of the brachiopod lophophore as characteristic of the phylum. One diverse group of Recent species, drawn from both the Inarticulata and Articulata and encompassing four families, can be described as having a spirolophous lophophore (spirolophes); that is, in the mature individual the lophophore is coiled into two simple arms which, in all known spirolophes except *Discinisca* and the closely related *Discina* (Rowell,

personal communication), point dorsally. Each arm (or brachium) bears a double row of ciliated filaments separated by the brachial groove from the lip. The side containing the lip is termed the frontal surface, and lateral cilia on the filaments beat across the length of the filament from the frontal toward the abfrontal surface (Atkins, 1956). Thus, the organism's food is filtered from water currents drawn perpendicularly to the length of the filament in a frontal to abfrontal direction. The interested reader is referred to Rudwick (1962) for a more complete account of the ontogeny and functioning of a variety of brachiopod lophophores.

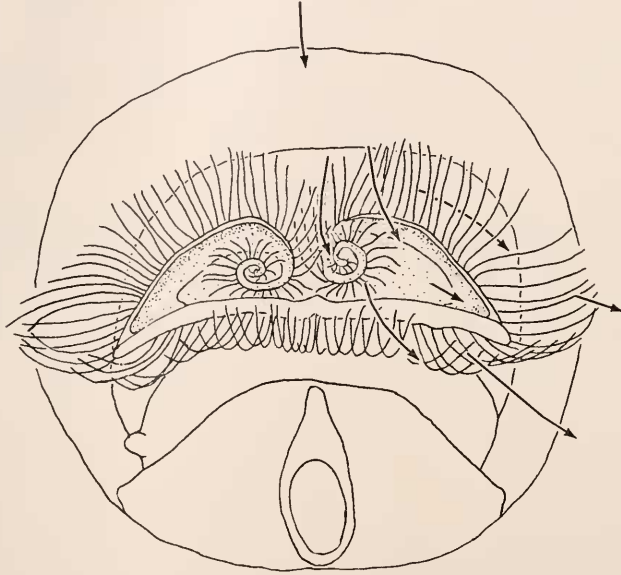


FIGURE 2. View of the expanded lophophore of *D. strigata* after removal of most of the ventral valve. The arrows represent the observed direction of water flow across the lophophore. The setae fringing the shell have been omitted.

The above arrangement of spiral arms, filaments, and ciliary beat specifies the feeding currents of most spirolophes. However, the ventrally-directed *Discinisca* spires have paleontological implications and the situation needs clarification.

The ventral valves of a number of *D. strigata* were partially removed and the lophophores allowed to relax fully, without narcotization. The water currents around the lophophore were then drawn as they appeared when viewed from the ventral aspect (Fig. 2). The apices of the slightly elevated spires are oriented ventrally (pointed toward the observer) and perhaps canted toward the median plane. The proximal whorl of each brachium appears greatly expanded, extending from the median plane almost to the lateral margin of the shell. The remaining more distal whorls comprise an insignificant portion of the spire, and, in fact, give rise to less than 20% of the total filament length. This figure was arrived at by measuring scattered filaments on the proximal and more distal whorls, and then multiplying their mean lengths (1.7 mm. and 0.5 mm., respectively) by their

numbers. Presumably, as the animals become larger, the disparity in allocation of filtering surface will continue to increase in favor of the proximal whorl.

In Figure 2 the frontal surface of the anterior filaments of the proximal whorl faces the observer, and in this region water currents pass normal to the plane of commissure (into the plane of the paper). These anteriormost filaments tend to lie against the mantle, forming an exhalant chamber leading to the posterolateral margins, dorsal to the main body of the lophophore. Water filtered by these filaments occupies this dorsal chamber. Similarly, if the ventral shell and mantle were present, those posterior filaments behind the mouth and closest to the observer, in lying against the mantle, would form another analogous exhalant chamber ventral to the lophophore. Some unfiltered water is also drawn into the distal portions of the spire and after being filtered must move dorsally and then laterally to join the main exhalant currents at the posterolateral margin of the valves. This previously filtered water inside each spire cannot mix with the unfiltered water because the filaments on the distal whorls are flexed abfrontally, touching the frontal surface of the next more proximal whorl. Most of the unfiltered water, however, passes along the expanded body of the proximal whorl and is filtered by the long filaments toward its lateral end.

As in most brachiopods, the filaments are incompletely ciliated, a tract being absent from the abfrontal surface. On excised filaments the lateral cilia were usually still, but the frontal ones continually beat toward the filament tips. Their normal beat would be toward the base and adjacent food groove, and this beat reversal can serve as a rejection mechanism.

At least two such rejection mechanisms are functional in the whole organism. The beat of the frontal cilia appears to be frequently reversed, since bands of mucus-bound particles were seen to be carried away from the brachial lip. And heavy particles, once inside the inhalant chamber, are pushed toward the chamber's margins by a coordinated flexing of the filaments, similar to that illustrated for *Lingula unguis* by Chuang (1956). Once at the edge these particles are probably expelled by a gentle clapping shut of the valves, as is known in the inarticulates, *Crania* (Orton, 1914) and *Glottidia* (Paine, unpublished), and some articulates (Rudwick, 1962).

In the normally feeding intact animal the slight gape of the valves is masked by a heavy fringe of long, barbed setae. The gross current pattern consists of a single, median inhalant current and paired, posterolateral exhalant ones. This pattern was never strongly developed, especially the exhalant currents, though in 20 specimens examined little variation was noticed. Not much current distortion is caused by the fringing setae which function, aside from being tactile elements, to catch and hold all but the finest water-drawn particles. In freshly collected specimens these setae were invariable festooned with detritus, particularly around the median inhalant aperture where they also reach their maximum length.

The nature of the currents inside the unopened animal can only be speculated on. Most likely all filaments of the proximal whorl touch the dorsal or ventral mantle surfaces. The tips of the longer, laterally placed filaments also probably intermesh completely in the restricted space of the mantle cavity, and in so doing form a tunnel trending laterally which encloses the main body of unfiltered water. The apices of the spires, enclosed within this tunnel, will be canted toward the median plane and possibly serve to orient the incoming current.

DISCUSSION AND CONCLUSION

A revival of interest in brachiopods, apparently focused on their feeding mechanism, has shown that most species can accurately be characterized by certain generalities. (1) In adult specimens the unfiltered water enters the mantle cavity as paired lateral currents and exits as a single median one, although in small individuals this external current pattern is usually reversed (Atkins, 1956; Rudwick, 1962). (2) The feeding currents are mainly produced by lateral cilia on the lophophoral filaments beating in a frontal to abfrontal direction, and the beat of these is seldom reversed. The report by Atkins (1960) of current reversal in the Megathyridae represents a momentary phenomenon; the usual beat is similar to that in other brachiopods and Atkins suggests (p. 471) that the reversal is elicited ". . . when strong cleansing action is called for." (3) And in spirolophous brachiopods the apices of the spires point dorsally.

Rudwick (1960a) has added further considerations. Filtered and unfiltered water may be kept separate by the arrangement of the lophophoral filaments. If this is achieved the animal possesses an "efficient" filtration system, if not, an "inefficient" one. All Recent brachiopods appear to be "efficient." Second, when unfiltered water occupies the center of the spire, the current system can be called inhalant, a condition characterizing most living spirolophes. An alternative inferred for *Discinisca* on topological grounds by Rowell (1961), and potentially equally efficient, is an exhalant system characterized by previously filtered water in the spire's center. Finally, Rudwick (1960a) has shown that all spirolophes can fall into either of two mutually exclusive categories. When the left brachium is viewed from its base toward its apex, it will coil either clockwise or counterclockwise. Among Recent species the latter group includes most spirolophes, the former only *Discinisca* (and presumably *Discina* as well). Both categories are well represented in fossil forms. Because the frontal surfaces of the brachia always face the mouth in early lophophoral stages, the counterclockwise group eventually develops an inhalant system and the clockwise group an exhalant one.

Rudwick's (1960a) contention that extinct spirolophes had only inhalant or exhalant systems of the construction presently extant has been challenged by Williams (1960) and Williams and Wright (1961). Much of what has been learned about *Discinisca* cannot help to resolve the central issues of this debate, which involve possible functions of structures only present in articulate brachiopods. However, because the left brachium of the *Discinisca* spire does coil clockwise, analogies drawn with extinct spire-bearers also characterized by clockwise coiling of their left brachium become more reasonable. And, through comparison with other spirolophes, those characteristics of the brachiopod feeding mechanism which are independent of lophophore orientation can be specified.

Perhaps the most germane observations are that the basic construction of the brachium has not been altered, and that the lateral cilia continue to beat in a frontal to abfrontal direction. However, the filaments of *D. strigata* are flexed abfrontally rather than frontally as in the inarticulates, *Lingula* (Chuang, 1956) and *Crania* (Atkins, in Rudwick, 1960a). The result of this alteration in flexure is that, given a ventrally-oriented spire, the feeding mechanism retains its efficiency. As Rowell (1961) has shown, if the filaments were flexed frontally, the inhalant and exhalant chambers could not be effectively isolated and the system would be

inefficient. The filaments, flexed as they are in *D. strigata*, form a system of inhalant and exhalant spaces which prevent previously filtered water from being recycled before it has been pumped from the animal. With the retention of the usual direction of ciliary beat and the maintenance of an efficient system, the gross current pattern can only be as it is.

D. strigata, however, shows a mixture of inhalant and exhalant systems. The water in the central portions of the spire already has been filtered, and on this basis this species must be considered at least partially exhalant. However, only 20% of the water is processed in this manner, the remainder probably passing along the tunnels formed by the lateral extension of the proximal whorl. The water here, in what would normally be the inside of the spire, is unfiltered and thus fits Rudwick's (1960a) description of inhalant systems. Blochmann's (1900; plate 8, Fig. 10) illustration of *D. lamellosa* suggests that a similar extension of the proximal whorl is found in another *Discinisca* species, and thus that a combination of inhalant and exhalant systems may typify the genus. This finding does not alter the logic of Rowell's (1961) conjecture based on a *Discinisca* lophophore in which all the whorls are concentric and similarly shaped, and where the filaments of the spire touch the next more proximal whorl. It should be emphasized that if the terms inhalant and exhalant current systems are simply descriptive, then *D. strigata* belongs to the exhalant group because only filtered water lies within the central axis of the spire. However, if total lophophore functioning is also considered, the dual interpretation of *D. strigata* is reasonable.

These results suggest that problems associated with gross current pattern, orientation of the spire, and the presence of inhalant or exhalant filtering systems can be minimized in typically constructed species, both extant and fossil. Reconstruction of the lophophores of fossil spirolophes can probably be satisfactorily based on the consistent properties of efficient filtering and unidirectional ciliary beat in a frontal to abfrontal direction.

This work was done during the tenure of a Sverdrup Postdoctoral Fellowship at the Scripps Institution of Oceanography. The author wishes to thank the following specialists for specific identifications: Dr. G. A. Cooper (brachiopod), Dr. W. D. Hartman (sponge), and Dr. R. Stohler (Mollusca). The paper has benefited from the suggestions of and critical reading by Dr. A. J. Rowell. Special recognition is due Mr. E. P. Chace, of the San Diego Museum of Natural History, for suggesting the locality where the *Discinisca* were found.

SUMMARY

1. Ecological observations on the brachiopod, *Discinisca strigata*, suggest that this species is zoned in shallow water in the northern Gulf of California. It occurs singly rather than in great clumps, and on the basis of a size-frequency distribution appears to be an annual.

2. Examination of the filter-feeding apparatus and its operation shows, despite an exceptional orientation of the lophophore, that there are a number of points in common with other brachiopods. The lateral lophophoral cilia beat in a frontal to abfrontal direction, and the current system through the animal is efficient.

3. The position of the inhalant aperture, relative direction of coiling of the left brachium, and orientation of the spire, although differing from those in other adult spirolophes, do not diminish the efficiency of operation. *D. strigata*, though showing a mixture of inhalant (80%) and exhalant (20%) filtering systems, is able to maintain its filtering efficiency, due to the disposition of filaments within the organism.

LITERATURE CITED

- ATKINS, D., 1956. Ciliary feeding mechanisms in brachiopods. *Nature*, **177**: 706-707.
- ATKINS, D., 1960. The ciliary feeding mechanism of the Megathyridae (Brachiopoda), and the growth stages of the lophophore. *J. Mar. Biol. Assoc.*, **39**: 459-479.
- BLOCHMANN, F., 1900. Untersuchungen über den Bau der Brachiopoden. Die Anatomie von *Discinisca lamellosa* (Broderip) und *Lingula anatina* Bruguière. II: 69-124. Jena.
- BLOCHMANN, F., 1908. Zur systematik und geographischen Verbreitung der Brachiopoden. *Zeitschr. f. Wiss. Zool.*, **90**: 596-644.
- BRODERIP, W. J., 1833. Descriptions of some new species of Cuvier's family of Brachiopoda. *Trans. Zool. Soc. London*, **1**: 141-144.
- CHUANG, S. H., 1956. The ciliary feeding mechanism of *Lingula unguis* (L.) (Brachiopoda). *Proc. Zool. Soc. London*, **127**: 167-189.
- CLOUD, P. E., 1948. Notes on Recent brachiopods. *Amer. J. Sci.*, **246**: 241-250.
- DAVIDSON, T., 1888. A monograph of Recent Brachiopoda. *Trans. Linn. Soc. London*, **4**: 1-248.
- HYMAN, L. H., 1959. The Invertebrates: Smaller Coelomate Groups. McGraw-Hill Book Co., Inc. New York.
- ORTON, J. H., 1914. On ciliary mechanisms in brachiopods and some polychaetes, with a comparison of the ciliary mechanisms on the gills of Molluscs, Protochordata, Brachiopods, and cryptocephalous Polychaetes, and an account of the endostyle of *Crepidula* and its allies. *J. Mar. Biol. Assoc.*, **10**: 283-311.
- RICHARDS, J. R., 1952. The ciliary feeding mechanism of *Neothyris lenticularis* (Desh.). *J. Morph.*, **90**: 65-91.
- ROWELL, A. J., 1961. Inhalant and exhalant feeding current systems in Recent brachiopods. *Geol. Mag.*, **98**: 261-263.
- RUDWICK, M. J. S., 1960a. The feeding mechanisms of spire-bearing fossil brachiopods. *Geol. Mag.*, **97**: 369-383.
- RUDWICK, M. J. S., 1960b. Correspondence. *Geol. Mag.*, **97**: 516-518.
- RUDWICK, M. J. S., 1962. Filter-feeding mechanisms in some brachiopods from New Zealand. *J. Linn. Soc. London*, **44**: 592-615.
- WILLIAMS, A., 1956. The calcareous shell of the Brachiopoda and its importance to their classification. *Biol. Rev.*, **31**: 243-287.
- WILLIAMS, A., 1960. Correspondence. *Geol. Mag.*, **97**: 514-516.
- WILLIAMS, A., AND A. D. WRIGHT, 1961. The origin of the loop in articulate brachiopods. *Palcont.*, **4**: 149-176.
- WILSON, D. P., 1958. Some problems in larval ecology related to the localized distribution of bottom animals. Perspectives in Marine Biology: 87-99. Univ. of California Press, Berkeley.